ACCEPTED FOR PUBLICATION IN: PLANT ECOLOGY (04-2018)

Foliar C, N, and P stoichiometry characterize successful plant ecological strategies in the Sonoran Desert.

Alejandro E. Castellanos[1*], José M. Llano-Sotelo[1], Luis I. Machado-Encinas[1], José E. López-Piña[1], Jose R. Romo-Leon[1], Jordi Sardans[2,3], Josep Peñuelas[2,3]

[1] Departamento de Investigaciones Científicas y Tecnológicas. Universidad de Sonora. Blvd. Luis Encinas y Rosales S/N, Col. Centro, Hermosillo, Sonora, México. C.P. 83000.

[2] CSIC, Global Ecology Unit CREAF-CSIC-UAB, Bellaterra, 08193 Catalonia, Spain.

[3] CREAF, Cerdanyola del Vallès, 08193 Catalonia, Spain.

[*] Corresponding author: alejandro.castellanos@unison.mx; acastell@guaymas.uson.mx

Abstract

Ecological processes are centered to water availability in drylands, however less known nutrient stoichiometry can help explain much of their structure and ecological interactions. Here we look to the foliar stoichiometry of carbon (C), nitrogen (N) and phosphorus (P) of 38 dominant plant species from the Sonoran Desert, grouped in four different functional types to describe ecological characteristics and processes. We found that foliar N, C:N, C:P and N:P stoichiometric ratios, but not P, were higher than those known to most other ecosystems and indicate P but not N limitations in leaves. Biological N fixers (BNF) had even higher leaf N concentrations, but bio-elemental concentrations and stoichiometry ratios were not different to other non-N fixing legume species which underscores the need to understand the physiological mechanisms for high N, and to how costly BNF can succeed in P-limiting drylands environments. Stoichiometry ratios, and to lesser extent elemental concentrations, were able to characterize BNF and colonizing strategies in the Sonoran Desert, as well as explain leaf attribute differences, ecological processes and biogeochemical niches in this dryland ecosystem, even when no direct reference is made to other water—limitation strategies.

KEYWORDS. Foliar stoichiometry; Nutrient-use efficiency; Drylands plants; Sonoran Desert; Biological nitrogen fixers; Invasive species.

Introduction

Drylands are widespread and cover more than 40 % of Earth's terrestrial surface (Dregne and Chou 1992; Evenari et al. 1985; Prăvălie 2016). Much studies of drylands studies have water pulses as drivers of major ecological functions (Huxman et al. 2004; Noy-Meir 1973; Ogle and Reynolds 2004), but the water-centered approach neglects many important processes and interactions in which nutrients play a more important role (Austin et al. 2004). Drylands contribute about a third of the net productivity of terrestrial ecosystems (Asner et al. 2004; Field et al. 1995), play an important role in the sequestration and storage of carbon (C) globally (Jackson 2000; Lal 2004; Ma et al. 2014) and have a noticeable impact on the seasonality of the global C cycle (Poulter et al. 2014), and nutrients are key drivers in all these ecosystem functioning processes. As such, a major concern now is that changes in nutrient cycles linked to current global trends of increasing dryness will have unknown consequences to productivity in arid ecosystems (Delgado-Baquerizo et al. 2017; Yuan and Chen 2015).

We have limited information on how nutrients may feed back to other plant physiological and ecological processes in drylands ecosystems. Different studies and climate change scenarios have established that soil nutrient cycles will uncouple with increasing drought, increasing nitrogen (N) depletion and phosphorus (P) availability (Delgado-Baquerizo et al. 2017; Delgado-Baquerizo et al. 2013; Yuan and Chen 2015). In plants under experimental drought however, both N and P concentrations decreased (Dijkstra et al. 2016; He and Dijkstra 2014). These potential conflicting results may require better knowledge on how N and P concentrations and their stoichiometry ratios, which may have important effects for nutrient cycling in drylands ecosystems. Understanding the stoichiometric relationships of C, N and P among different species and functional groups should help to understand many of today's physiological and ecological unknowns of species interactions in drylands ecosystems, that the water-centered approach has not resolved (Austin 2011).

Nitrogen is a key element that limits productivity in arid ecosystems (Skujins 1981), but it has been largely ignored (Austin 2011). Drylands are known to be limited by low soil N (Nieder and Benbi 2008; West and Skujins 1978) and P concentrations (Kajtha et al. 1987; Schlesinger 1997), when water is available. However, despite the known low N soil concentrations, the leaves of drylands species are known to have higher N concentrations (Skujins 1981; West 1981; West and Klemmedson 1978; West and Skujins 1978), although some controversy still remains (Killingbeck and Whitford 1996; Reich and Oleksyn 2004). Global surveys contain limited data specific to drylands species and document high foliar N concentrations (Killingbeck and Whitford 1996; Tao et al. 2016), which calls for more survey studies to characterize drylands plant species elemental nutrient concentrations and stoichiometry ratios.

A water—centered approach may have missed to explain how species and functional groups interact in drylands ecosystems. Diverse strategies have been documented in different species and growth forms for N uptake (Belnap et al. 2001; Berdugo et al. 2014; Virginia et al. 1992), reabsorption (Killingbeck 1993, 1996), mineralization (Reyes-Reyes et al. 2003), use and loss (Schlesinger and Pilmanis 1998; Schlesinger et al. 2000), as well as P soil and plant heterogeneous distribution (Schlesinger and Pilmanis 1998), and how those nutrients drive the above- and below-ground interactions in drylands ecosystems (McCulley et al. 2004). A key to understand drylands ecosystems

nutrient cycling processes and species interactions is to know the species leaf concentration and stoichiometry ratios.

Here, we determined total C, N and P concentrations and stoichiometric ratios in the leaves of 38 dominant species in the southwestern region of the Sonoran Desert in central Sonora. We grouped plant species in different functional groups, for growth form, leaf habit, N-fixing ability and colonizing capability. We used these functional groups to test how foliar stoichiometry traits can help to explain successful ecological strategies in drylands environments.

Methodology

The study area was in northwestern Mexico (28-30°N, 110-112°W) in the Sonoran Desert region of central Sonora, Mexico (Figure 1). We chose thirty one sites within the boundaries of five major proposed conservation areas. The climate in the region is hot and dry, with mean annual temperatures from 20 to 24 °C and annual rainfall between 135 and 555 mm, mostly during the summer monsoon (80-90%) from July to September, with fall or winter precipitation during some years (Brito-Castillo et al. 2010). Temperatures usually remain above freezing during the winter, although some frosts have been reported in recent years that have led to some tree mortality. The soils at the sites were mostly Lithosols, Eutric Regosols and Xerosols (INIFAP-CONABIO 2001), consistently with more than 80% sand, although the soils differ at some microsites.

Vegetation sampling and functional groups

The plant communities in the region are dominated by trees and shrubs with variable herbaceous coverage during the growing season in different years. The sampled dominant plant associations were Mezquital (*Prosopis velutina and Olneya tesota*), microphyllous desert shrublands (*Larrea tridentata*, *Ambrosia dumosa* and *A. cordifolia*) and subtropical shrublands (*Lysiloma divaricata and Acacia cymbispina*) (Brown 1982; INEGI 2000; Shreve and Wiggins 1964).

We sampled the dominant species from 31 sites with native vegetation and no major signs of disturbance. We selected species for nutrient and stoichiometric comparisons from the two or three most dominant height strata using the *relevé* method. Dominance/abundance was determined for each site from categories of species coverage/abundance (Mueller-Dumbois and Ellenberg 1974) obtained along three 150-200 m transects at each site. The species representing up to 80% of the cover for the community on each transect were identified and assigned to the various functional groups.

At each site, the most dominant species were almost always different. We compared all different species and then assigned them to different functional groups. We compared functional groups for growth form (trees, shrubs, subshrubs, herbs and grasses, and succulent cacti), foliar phenology (deciduous, evergreen and succulent cacti), colonizing capability (invasive, pioneers and other native species) and biological N fixation (Fabaceae and Mimosaceae, as BNF species) for statistical differences in elemental and stoichiometric ratios. All sites were native, but most had some degree of cattle grazing. The spontaneous presence of the exotic buffelgrass (*Cenchrus ciliaris*) was found at some of the sites (<1-5%) and was included in the analyses. Vegetation sampling, local knowledge (COTECOCA 2002), a regional floristic database (SEINET) and previous field experience were used to determine

123 the colonizing capability of the species. Such strategy is one of the most important traits in desert species after local
124 disturbances.
125 Fully exposed mature leaves were collected from each of the dominant species, only during the peak of the
126 growing season in two different years. Once collected, leaves were immediately transferred to plastic bags
127 containing a wet paper towel, stored in an ice chest, transported to the laboratory and stored at -4 °C until leaf area
128 was measured. The areas of fresh leaves were measured with a scanner using ImageJ (Schneider et al. 2012), dried
129 in a ventilated oven at 60 °C for 48 h and stored in a desiccator to equilibrate and then weighed. The leaf mass area
130 (LMA), the projected area per unit dry weight, was then obtained.
131
132 *Laboratory analysis*
133 The same dried leaf samples were ground to a 40-mesh size. Total foliar C and N concentrations were measured
134 with an Elemental Analyzer (Perkin-Elmer CHNS/O 2400, Waltham, USA) after sample combustion in an oxygen
135 atmosphere at 925 °C. Total Kjeldahl P was also obtained from these ground samples after acid digestion with
136 copper sulfate as a catalyst and an ammonium molybdate colorimetric reaction, using an automated rapid-flow
137 analyzer (SEAL, Norderstedt, Germany). For each species, mean nutrient concentrations were obtained from
138 determinations in leaves from three individuals. C, N and P concentrations and stoichiometric ratios are expressed as
139 mass units (mg g^{-1}) and fractions for comparison with most recent studies.
140
141 *Statistical analysis*
142 All nutrient concentration and stoichiometric data were $\log_{10}$-transformed for ANOVAs and correlation analyses as
143 suggested by Sterner and Elser (2002). Since most of our data exhibited non-normal distribution within species, bio-
144 elemental concentrations and their ratios were $\log_{10}$ transformed to meet normality assumptions. Nutrient and
145 stoichiometry ratio differences between species, growth form, leaf habit and BNF capacity were determined using
146 ANOVAs of the $\log_{10}(X)$ transformed data and HSD-Tukey's a posteriori tests for differences. The data were
147 retransformed after the analyses. ANOVAs statistical analyses were performed using JMP 9 (SAS Institute Inc.,
148 Cary, NC, USA). We also performed discriminant functional analyses (DFAs) to determine whether the
149 concentrations of C, N and P and their ratios could discriminate among the functional groups for detecting possible
150 differences in the use of these three bio-elements, depending on the ecological and growth strategies of the species.
151 DFA assumes that the used variables are normally distributed (McLachlan et al. 2004). $\text{Log}_{10}(X)$ transformation of
152 all variables was needed to normalize them. DFA is a supervised statistical algorithm that will derive an optimal
153 separation between groups established a priori by maximizing between-group variance while minimizing within-
154 group variance (Raamsdonk et al. 2001). The DFAs were performed using Statistica 8.0 (StatSoft, Inc., Tulsa,
155 USA).
156
157 **Results**
158 Mean cover among sites was obtained independently for the tree, shrub and herb strata. Mean percent coverage was
159 <20% for any of the strata we sampled. Our *relevés* indicated that on average, more land was covered by shrubs than

trees, and BNF species, although the number of BNF species was lower (Table 1).

Stoichiometry differences among species

Foliar C concentrations varied from 359.7 to 486.8 mg C g^{-1} for all species, with lowest C in the photosynthetic stems of cholla cacti. Those same species were five to eight-fold different in foliar N (9.03 to 40.45 mg N g^{-1}) and P concentrations (0.60 to 5.06 mg P g^{-1}), and were consequently highly variable (427.5 ± 68.5 mg C g^{-1}, 23.0 ± 9.0 mg N g^{-1} and 1.6 ± 0.9 mg P g^{-1}). A significant but low correlation and slope was found between species foliar N and P (Figure 2). N and P in the photosynthetic tissues (succulent stems) of cholla cactus species (*Cylindropuntia versicolor*) were the lowest, and the highest in the subshrub *A. cordifolia* (40.4 ± 5.6 mg N g^{-1}, 2.8 ± 0.5 mg P g^{-1}; Supplemental Table S1). A weak negative correlation for leaf C:N ratio and P was found (r^2=0.164, Figure 3).

Differences among growth forms and leaf habits

Elemental concentrations were significantly different among growth forms (Table 2). Foliar N concentration were higher in shrubs, trees and subshrubs (25.9 ± 0.78 mg N g^{-1}) than herbs and grasses (15.0 ± 1.07 mg N g^{-1}) and cacti (11.01 ± 0.87 mg N g^{-1}). In contrast, mean foliar P mass concentrations were significantly higher in subshrub, herbs and grasses (2.1 ± 0.16 mg P g^{-1}) than trees, shrubs and cacti (F=5.6, p<0.0003). C:P ratios were significantly higher in trees (355.01 ± 19.1).

Species with deciduous leaves were more common (30 species) and abundant than evergreens (6) and succulents (2). C, N and P concentrations were always lowest in the photosynthetic tissues of succulent cholla cacti, while in deciduous species C was lower (F=91.9, p<0.0001) and P higher (F=3.9, p<0.022) compared to evergreens, but no differences in N concentrations were found (Table 2). In evergreens, C:P ratio was higher (380.7 ± 30.2), but for deciduous and evergreens C:N was lower (F=47.4, p<0.0001) and N:P higher than in the photosynthetic tissues of Cholla cacti.

Stoichiometry of BNF and pioneers

We tested for stoichiometry differences in biological nitrogen fixers (BNF), legumes and other Sonoran Desert species. N leaf concentration in BNF species was much higher than overall species and functional group means, but was not correlated to P, although a significant negative correlation was found between C:N and P (F=10.7, p≤0.002, r^2=0.189). C:N ratio was significantly lower and N:P higher in BNF species (F=10.1, p<0.0018; Table 2).

Grouped by their capability to colonize post-disturbance habitats, invasive species had the lowest foliar C and N but highest P concentrations than non-invasive species (Table 2). Invasive species had higher C:N ratios (35.38 ± 2.74; F=59.00, p<0.0001), despite their low foliar C and N concentrations, and the lowest N:P ratios (8.0 ± 1.61; F=17.93; p<0.0001). Because the large variability in C:P ratios, there were no significant differences between colonizing capability.

BNF and colonizing capabilities were clearly differentiated along the stoichiometric-ratio axes. The discriminant functional analyses (DFA) showed significant squared Mahalanobis distances among functional groups with respect to their foliar C, N and P concentrations and stoichiometry ratios when both colonizing potential

(pioneers, invasives, natives) and N-fixation capability ecological groups (non-N-fixing pioneers, N-fixing pioneers, non-N-fixing invasives, non-N-fixing natives and N-fixing natives) were considered (Figure 4). The DFA found that invasive species had the highest C:N ratios but lowest N concentrations and N:P ratios (Figure 4). Bio-elemental composition and C:N and C:P ratios differed in pioneers, with higher C:N ratios and C and N concentrations, but lower C:P ratios in BNF pioneers.

Discussion

Bio-elemental C, N and P concentrations and their stoichiometric ratios were highly variable and skewed. Elemental and nutrient investment in leaves are adaptive traits in plants to ensure the C gains over their life span (Harper 1989). Such adaptive strategies allow plants to adjust bio-elemental stoichiometric ratios to optimize the investment of nutrients and energy to the photosynthetic, light capture, survival and defense functions in the leaves (Westoby and Wright 2006; Wright et al. 2004). Here we analyzed the foliar C, N and P concentrations and stoichiometric ratios from 38 plant species of the Sonoran Desert, and their ecological significance when grouped in four different plant functional types.

Species had a large variability in C, N and P concentrations (Supplemental Table S1). We found ten- to twenty-fold differences in elemental concentrations but only about three- to five-fold in the stoichiometric ratios in all sampled individuals. Other studies have reported species variability in elemental concentrations, three- to ten-fold differences in N and P concentrations in wetland species (Koerselman and Meuleman 1996), and up to 20-fold (N) and 30-fold (P) in global analyses (Elser et al. 2010). Intra-specific differences in all those studies were highly skewed and were larger than inter-specific differences at different sites (Koerselman and Meuleman 1996; Reich and Oleksyn 2004), even when changes in species composition were considered (Yang et al. 2016). The large intra-specific variation we found in the elemental composition of Sonoran Desert species may indicate high homeostatic plasticity, considered to be advantageous in unpredictable and drylands environments (Elser et al. 2010; Sistla and Schimel 2012; Sterner and Elser 2002).

Our data identified patterns of high N foliar concentration and significant differences among species and functional groups, although high leaf N in drylands has been a matter of controversy. We found an overall mean N concentration (23.66 ± 0.52 mg N g^{-1}) that is higher to the mean of 20.1 ± 8.7 mg N g^{-1} in global databases (Elser et al. 2010; Reich and Oleksyn 2004; Wright et al. 2004), similar to those from grasslands (24 mg N g^{-1}), and drylands like the Taklamakan (24.7 ± 1.8 mg N g^{-1}) and higher than the Aixa Desert (10.65 ± 1.4 mg N g^{-1}) in China (Tao et al. 2016). There are reports of high N in leaves of desert species (Skujins 1981; West 1981; West and Klemmedson 1978; West and Skujins 1978), while others have contended such findings (Killingbeck and Whitford 1996; Lamont et al. 2002). Some studies suggest that foliar N should be low because limiting N and volumetric soil moisture concentrations in arid soils which may constraint nutrient uptake and transport within the plant.

In contrast to N, species had low P concentrations. We found that foliar P was lower (1.62 ± 0.06 mg P g^{-1}) than mean concentrations (1.77 to 1.90 mg P g^{-1}) in extensive global data sets (Elser et al. 2007; He et al. 2008; Reich and Oleksyn 2004; Tao et al. 2016; Wu et al. 2012). In our data, although N and P were co-limited (Figure 2),

234 we found a weak N - P correlation compared to other studies (Elser et al. 2010; Reich et al. 2010), and a lower slope,
235 but the specific mechanisms by which this may happen, deserve to be determined. We encourage complimentary
236 surveys, physiological studies and stoichiometric approaches to gain better understanding of the N and P
237 relationships in leaves of drylands species, in particular those in the Sonoran Desert, although some initial results
238 suggest that nitrogen fixing species contribute to such weak correlation.
239
240 *High N and P limitation in leaves of BNFs and legumes*
241 The abundance and dominance of legumes (Mimosaceae, Fabaceae, Caesalpinaceae), some of which are known
242 BNFixers (Felker and Clark 1980; Felker and Clark 1981; Shreve and Wiggins 1964; Van Devender et al. 2010;
243 Virginia and Jarrell 1983), is an important characteristic of the plant communities of the South - Southeastern
244 regions of the Sonoran Desert, as it merges with the tropical deciduous forest biogeographic ecotone (Brown 1982;
245 Castellanos et al. 2010; Rzedowski 1993; Shreve and Wiggins 1964). We found that about 15% of the dominant
246 species we sampled were legumes and contributed with about a third of the mean coverage at the sites, although
247 their species richness was lower than non-fixing species (Table 1).
248 As found for species in general, BNF species had leaf N (mass and area) concentrations that were
249 significantly higher to the species mean (Table 2). High leaf N in BNF species are known from tropical, dry-forests,
250 drylands and in global databases (Adams et al. 2016; Hedin et al. 2009; Vergutz et al. 2012; Wolf et al. 2017). The
251 benefits of higher N in leaves is related to high photosynthetic capacity in most C_3 species (Evans 1989; Field et al.
252 1983), although more recent evidence suggest that N_{area} may not be related to photosynthetic performance in BNF
253 species (Adams et al. 2016; Funk et al. 2013). As in other C_3 species (Adams et al. 2016; Cernusak et al. 2013; Field
254 et al. 1983), high N_{area} has been related in the past with high intrinsic water use efficiency (A_{sat}/g_s) in BNF species
255 (Adams et al. 2016; Field et al. 1983), the increase in N-based defensive compounds (Coley et al. 1985), and
256 physiological flexibility under limiting and heterogeneous N soil availability (Wolf et al. 2017), but see (McKey
257 1994), and reduced transpiration that may limit nutrient uptake (Cramer et al. 2009).
258 But high N in leaves is not only the outcome of nitrogen fixation, as we found no elemental and
259 stoichiometric differences between legumes and BNF species (Table 3). Some studies suggest that all legumes, and
260 not only BNF, have hard-wired intrinsic physiological and phylogenetic mechanisms that allow for high N in leaves
261 (Fyllas et al. 2009), as we found in Sonoran Desert legumes, although other studies have found differently (Wolf et
262 al. 2017).
263 High N in leaves may reduce the use efficiency of nitrogen in BNF (Menge et al. 2008) as P limits nitrogen
264 fixation. Stoichiometry ratios may be used as proxys for elemental C, N or P use efficiencies. In the Sonoran Desert,
265 high N:P ratios in BNF suggests that P and not N may be the most limiting resource (Table 2). Because fixing
266 nitrogen is energy expensive and requires large amounts of P which is limiting under arid conditions (Delgado-
267 Baquerizo et al. 2017; Dijkstra et al. 2016), the N:P ratio is an important stoichiometric variable that indicates N
268 (N:P <14) or P (N:P >16) limitation (Aerts and Chapin 2000; Koerselman and Meuleman 1996). We found that
269 almost 92% of the species in our study had P-limited leaves (mean N:P = 16.8 ± 0.73; Table S1), much stronger than
270 in other regional and global data sets (Niklas and Cobb 2005; Reich and Oleksyn 2004; Yang et al. 2016).

High N and N:P ratios because low P in leaves indicate that Sonoran Desert species and functional types are much more limited by P than N. BNF species may not be viable in arid areas with limited soil P, due to the high energy costs and P concentrations required to build and maintain bacterial nodules, N fixation and foliar concentrations (Phillips 1980; Vance and Heichel 1991), and their presence may be paradoxical in drylands as in other subtropical regions (Hedin et al. 2009). How N fixation can succeed under limited P and drought conditions is not completely understood yet, it may include processes to lower metabolic costs by synthesis of ureides that allow N export from nodules (Valentine et al. 2017), increase allocation of P from roots to shoots, and enhancing root phosphatase activity to increase P availability in the soil (Houlton et al. 2008; Png et al. 2017; Tapia-Torres et al. 2015). All three strategies to enhance P availability and competitive ability of BNF may be important, but more experimental studies may help understand which of those mechanism allow the success of BNF in the Sonoran Desert and other dryland environments.

C:N stoichiometry ratio and colonizing capability

Higher C:N ratios in leaves may be correlated with the physiological and ecological strategies required for maximizing C gain (Harper 1989; Wright et al. 2004) and light-use (Sterner and Elser 2002) for any given N in the leaf, which may be expressed as stoichiometry ratio or efficiency. The light:nutrient hypothesis states that C:N ratios are higher in bright environments, because gains in photosynthetic C increase for any given N concentration (Sterner and Elser 2002; Sterner et al. 1997).

Even though we did not measure photosynthetic performance, we found that foliar C:N ratios, but not N concentrations, were significantly higher in pioneer-colonizers (native invasive species *sensu* Alpert et al. 2000) and invasives (Figure 4). We found that high C:N ratios were found in two contrasting growth strategies, e.g. the pioneer - photosynthetic CAM cholla cacti (37.8 ± 2.62) and the invasive exotic C_4 buffelgrass (35.4 ± 2.74), both with some of the lowest N concentrations in photosynthetic tissues (11.0 ± 0.9 and 14.6 ± 1.03 mg N g^{-1} respectively, Table 2). The high C:N stoichiometry ratio in these two contrasting strategies may indicate a closer relationship with a high light:nutrient efficiency hypothesis for drylands plant species (Sterner et al. 1997), even though their reported photosynthetic and growth rates may be at opposite extremes, higher for the invasive buffelgrass (Castellanos et al. 2010; Larcher 1995), and lowest in cholla cacti (Nobel and Bobich 2002; Nobel et al. 1991; Patten and Dinger 1969; Tschirley et al. 1964). It is to note that the buffelgrass and cholla cactus have contrasting photosynthetic pathways, C_4 and CAM, and because they both share a more effective concentrating CO_2 mechanism in photosynthesis than in C_3 species (the phosphoenolpyruvate (PEP) carboxylase) (Osmond et al. 1982; Patten and Dinger 1969), their investments in other carboxylase enzymes (and N) may be much lower (Funk et al. 2013; Sage et al. 1987).

C:N but not C:P stoichiometry ratios were differentiated among successful pioneers and invaders (Figure 4). Species in those groups, pioneers and invaders, have different photosynthetic pathways, e.g. C_3 (*Encelia farinosa*), CAM (*Cylindropuntia fulgida*) and C_4 (*Cenchrus ciliaris*), all with previously reported high water use efficiency mechanisms (Castellanos et al. 2010). As CAM species seem to grow slowly, while the C_3 and C_4 species grow faster, growth rates does not seem to be a common characteristic of these group of successful pioneers and invader species, however it is interesting that their N:P ratios were low, a stoichiometry ratio characteristic linked to

fast grown species, as found for the invasive buffelgrass.

High photosynthetic rates and photosynthetic nitrogen use efficiency (PNUE), a ratio of photosynthetic C gains per unit of N invested in leaves, has been documented for invasive species (McDowell 2002; Peñuelas et al. 2010), and has been related to invasive success in nutrient-limited environments (Funk 2013; Funk and Vitousek 2007). High C:N stoichiometry ratios may not result in higher PNUE, particularly in arid environments, because other processes such as photorespiration, photoinhibition, growth and maintenance respiration and defense mechanisms may account for some of the foliar N (Demmig-Adams and Adams 2006; Lea and Morot-Gaudry 2001; Leegood et al. 1995; Osnas et al. 2013), but this needs to be documented further. Similar to our findings, other studies have found increase in C:N foliar stoichiometry with drought (He and Dijkstra 2014; Sardans et al. 2008; Sardans et al. 2012), even though their physiological links are inconclusive and require further understanding of the physiological and ecological mechanisms that relate stoichiometry ratios and colonizing ability in hot arid ecosystems.

Our data support the idea that high C:N ratios may be associated with the light:nutrient-use efficiency hypothesis but not photosynthetic N or P use efficiency in arid environments, although in some cases both mechanisms may coincide. For example, our results grouped invasive and pioneer functional groups with C:N ratios that were higher than non-invasives, while BNF species differentiated in their C:P and N:P stoichiometry ratios, such that functional groups were distributed along different biogeochemical niches (Peñuelas et al. 2010; Sardans and Peñuelas 2014). For the invasive grasses buffelgrass (This study; Castellanos et al. 2010) and Lehmann lovegrass in the Sonoran Desert (Ignace et al. 2007), low foliar N concentration and high C:N stoichiometry (a proxy measure of NUE) were consistent with the resource use efficiency hypothesis for invasive success in nutrient-limited habitats (Funk 2013; Funk and Vitousek 2007), which seem to hold true also, for the native - pioneer species in the Sonoran Desert environment. We have shown that elemental biogeochemical niche hypothesis can differentiate pioneers from invasives, as well as BNF N—resource acquisition strategies in drylands environments.

Conclusions

In our study, the N, P and stoichiometric ratios were powerful tools to differentiate among plant functional groups and ecological strategies in drylands environments like in the Sonoran Desert. High C:N foliar ratios were able to differentiate invasive and pioneers in Sonoran Desert species, while N concentrations and N:P ratios were bigger for BNFixers than other non-legume native species. High N, C:N and N:P stoichiometry ratios may require further physiological and ecological studies to better understand their role in the differentiation of species, as they have been correlated to water, N, and P use efficiencies, and how they influence the structure and composition of dryland plant communities.

Stoichiometry relationships clearly differentiated biogeochemical niches of colonizing, pioneers and BNFs functional groups of Sonoran Desert species. Leaf stoichiometry ratios of dryland functional groups seem to be linked to high N and P use efficiency of their leaves and photosynthetic organs, although they may or may not be associated with higher photosynthetic performance or slow growth rates, as has been reported in non—limiting environments. Further studies linking stoichiometry to physiology in water-limited environments should help to

345 determine how foliar nutrient concentrations and C:element (N and P) stoichiometry ratios may relate and respond
346 to investments in photosynthetic machinery. Investments in photosynthetic performance, including photorespiration,
347 photo-protection and respiration, and other light and energy capture processes, may increase their nutrient use
348 efficiencies to enhance their performance and differentiate their ecological strategies. Given the different scenarios
349 of climate change and the effects of N and P decoupling in soil, linking plant stoichiometry ratios to water, light and
350 nutrient use efficiencies with their soil environment, may prove to be stronger tools in the future, to assess
351 ecological strategies and species interactions in drylands ecosystems.
352
353
354 **Acknowledgements**
355 The manuscript benefited from the reading and suggestions from two anonymous reviewers. AEC and JRRL
356 acknowledge the support of grants from CONABIO (LI005) and CONACYT (CB223525-R and INF2012/1-
357 188387) and support from UNISON to JMLl. Scholarships were granted by CONACYT to IM and JEP for their BSc
358 dissertations. JS and JP acknowledge the support of grants from the European Research Council Synergy ERC-SyG-
359 2013-610028 IMBALANCE-P, the Spanish Government CGL2016-79835-P- and the Catalan Government
360 SGR2014-274. We thank C. Trujillo, R. Méndez, D.E. Moreno, G. Díaz, A.K. Bustamante and the ecophysiology
361 group for field and lab support.
362
363
364
365 **Bibliography**
366
367 Adams MA, Turnbull TL, Sprent JI, Buchmann N. 2016. Legumes are different: Leaf nitrogen, photosynthesis, and
368 water use efficiency. Proceedings of the National Academy of Sciences 113: 4098-4103.
369 Aerts R, Chapin FS. 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns.
370 Adv. Ecol. Res. 30: 1 - 67.
371 Alpert P, Bone E, Holzapfel C. 2000. Invasiveness, invasibility and the role of environmental stress in the spread of
372 non-native plants. Perspectives in Plant Ecology, Evolution and Systematics 3: 52-66.
373 Asner GP, Elmore AJ, Olander LP, Martin RE, Thomas Harris A. 2004. Grazing systems, ecosystem responses, and
374 global change. Annual Review of Environmental Resources 29: 261-299.
375 Austin AT. 2011. Has water limited our imagination for aridland biogeochemistry? Trends in Ecology & Evolution
376 26: 229-235.
377 Austin AT, Yahdjian L, Stark JM, Belnap J, Porporato A, Norton U, Ravetta DA, Schaeffer SM. 2004. Water pulses
378 and biogeochemical cycles in arid and semiarid ecosystems. Oecologia 141: 221-235.
379 Belnap J, Prasse R, Harper KT. 2001. Influence of biological soil crusts on soil environments and vascular plants.
380 In: Belnap J, Lange OL (eds), Biological soil crusts: Structure, function, and management. Springer-Verlag,
381 Berlin, pp. 281-300.
382 Berdugo M, Soliveres S, Maestre FT. 2014. Vascular plants and biocrusts modulate how abiotic factors affect wet-
383 ting and drying events in drylands. Ecosystems 17: 1242-1256.
384 Brito-Castillo L, Crimmins MA, Díaz SC. 2010. Clima. In: Molina-Freaner FE, Van Devender TR (eds), Diversidad
385 Biológica de Sonora. UNAM - CONABIO, México, D. F., pp. 73-96.
386 Brown DE. 1982. Biotic communities of the American Southwest.- United States and Mexico. Desert Plants 4: 1-
387 342.
388 Castellanos AE, Bravo LC, Koch GW, Llano JM, Lopez D, Mendez R, Rodriguez JC, Romo JR, Sisk T, Yanes G.
389 2010. Impactos Ecologicos por el Uso del Terreno en el Funcionamiento de Ecosistemas Aridos Semi-

Aridos de Sonora. In: Molina-Freaner F, Van Devender TR (eds), Diversidad Biologica del Estado de Sonora. CONABIO - UNAM., México, D. F., pp. 157 - 186.
Cernusak LA, Ubierna N, Winter K, Holtum JAM, Marshall JD, Farquhar GD. 2013. Environmental and physiological determinants of carbon isotope discrimination in terrestrial plants. New Phytol. 200: 950-965.
Coley PD, Bryant JP, Chapin FS. 1985. Resource availability and plant antiherbivore defense. Science 230: 895-899.
COTECOCA. 2002. Diagnóstico de los agostaderos del Estado de Sonora. COTECOCA, Hermosillo, Sonora, p. 52.
Delgado-Baquerizo M, Eldridge DJ, Maestre FT, Ochoa V, Gozalo B, Reich PB, Singh BK. 2018. Aridity Decouples C:N:P Stoichiometry Across Multiple Trophic Levels in Terrestrial Ecosystems. Ecosystems 21: 459-468.
Delgado-Baquerizo M, Maestre FT, Gallardo A, Bowker MA, Wallenstein MD, Quero JL, Ochoa V, Gozalo B, García-Gómez M, Soliveres S, García-Palacios P, Berdugo M, Valencia E, Escolar C, Arredondo T, Barraza-Zepeda C, Bran D, Carreira JA, Chaieb M, Conceição AA, Derak M, Eldridge DJ, Escudero A, Espinosa CI, Gaitán J, Gatica MG, Gómez-González S, Guzman E, Gutiérrez JR, Florentino A, Hepper E, Hernández RM, Huber-Sannwald E, Jankju M, Liu J, Mau RL, Miriti M, Monerris J, Naseri K, Noumi Z, Polo V, Prina A, Pucheta E, Ramírez E, Ramírez-Collantes DA, Romão R, Tighe M, Torres D, Torres-Díaz C, Ungar ED, Val J, Wamiti W, Wang D, Zaady E. 2013. Decoupling of soil nutrient cycles as a function of aridity in global drylands. Nature 502: 672-676.
Demmig-Adams B, Adams WW. 2006. Photoprotection in an ecological context: the remarkable complexity of thermal energy dissipation. New Phytol. 172: 11-21.
Dijkstra FA, Carrillo Y, Aspinwall MJ, Maier C, Canarini A, Tahaei H, Choat B, Tissue DT. 2016. Water, nitrogen and phosphorus use efficiencies of four tree species in response to variable water and nutrient supply. Plant and Soil 406: 187-199.
Dregne HE, Chou N-T. 1992. Global desertification dimensions and costs. In: Dregne H (ed), Degradation and Restoration of Arid Lands. Texas Tech University, Lubbock, Tx.
Elser JJ, Bracken MES, Cleland EE, Gruner DS, Harpole WS, Hillebrand H, Ngai JT, Seabloom EW, Shurin JB, Smith JE. 2007. Global analysis of nitrogen and phsphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol. Lett. 10: 1135-1142.
Elser JJ, Fagan WF, Kerkhoff AJ, Swenson NG, Enquist BJ. 2010. Biological stoichiometry of plant production: metabolism, scaling and ecological response to global change. New Phytol. 186: 593-608.
Evans JR. 1989. Photosynthesis and nitrogen relationships in leaves of C_3 plants. Oecologia 78: 9-19.
Evenari M, Noy-Meir I, Goodall DW (eds. 1985. Hot Deserts and Shrublands. Elsevier, Amsterdam.
Felker P, Clark PR. 1980. Nitrogen fixation (acetylene reduction) and cross inoculation in 12 Prosopis (mesquite) species. Plant and Soil 57: 177-186.
Felker P, Clark PR. 1981. Nodulation and nitrogen fixation (acetylene reduction) in desert ironwood (*Olneya tesota*. Oecologia 48: 292-293.
Field CB, Merino J, Mooney HA. 1983. Compromises between water-use efficiency and nitrogen-use efficiency in five species of California evergreens. Oecologia 60: 384-389.
Field CB, Randerson JT, Malmstrom CM. 1995. Global Net Primary Production - Combining Ecology and Remote-Sensing. Remote Sens. Env. 51: 74-88.
Funk JL. 2013. The physiology of invasive plants in low-resource environments. Conservation Physiology 1: 1-17.
Funk JL, Glenwinkel LA, Sack L. 2013. Differential allocation to photosynthetic and non-photosynthetic nitrogen fractions among native and invasive species. PLoS ONE 8: e64502.
Funk JL, Vitousek PM. 2007. Resource-use efficiency and plant invasion in low-resource systems. Nature 446: 1079-1081.
Fyllas NM, Patino S, Baker TR, Bielefeld Nardoto G, Martinelli LA, Quesada CA, Paiva R, Schwarz M, Horna V, Mercado LM. 2009. Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate. Biogeosciences 6: 2677-2708.
Harper JL. 1989. The value of a leaf. Oecologia 80: 53 - 58.
He J-S, Wang L, Flynn DFB, Wang X, Ma W, Fang J. 2008. Leaf nitrogen : phosphorus stoichiometry across Chinese grassland biomes. Oecologia 155: 301-310.
He M, Dijkstra FA. 2014. Drought effect on plant nitrogen and phosphorus: a meta−analysis. New Phytol. 204: 924-931.
Hedin LO, Brookshire ENJ, Menge DNL, Barron AR. 2009. The nitrogen paradox in tropical forest ecosystems. Annual Review of Ecology, Evolution, and Systematics 40: 613-635.

445 Houlton BZ, Wang Y-P, Vitousek PM, Field CB. 2008. A unifying framework for dinitrogen fixation in the terres-
446 trial biosphere. Nature 454: 327-330.
447 Huxman TE, Snyder KA, Tissue D, Leffler AJ, Ogle K, Pockman WT, Sandquist DR, Potts DL, Schwinning S.
448 2004. Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. Oecologia 141: 254-268.
449 Ignace DD, Huxman TE, Weltzin JF, Williams DG. 2007. Leaf gas exchange and water status responses of a native
450 and non-native grass to precipitation across contrasting soil surfaces in the Sonoran Desert. Oecologia 152:
451 401-413.
452 INEGI. 2000. Inventario Forestal Nacional Serie III. INEGI.
453 INIFAP-CONABIO. 2001. Edafología, Esc: 1:250,000. CONABIO, México, D.F., p. Edafología. Escalas 1:250000
454 y 250001:1000000. México.
455 Jackson RB. 2000. Belowground processes and global change. Ecol. Appl. 10: 397-398.
456 Kajtha K, Wishampel J, Schlesinger WH. 1987. Phosphorous and pH tolerances in the germination of the desert
457 shrub Larrea tridentata (Zygophyllaceae. Madroño 34: 63 - 68.
458 Killingbeck KT. 1993. Nutrient resorption in desert shrubs. Revista Chilena de Historia Natural 66: 345 - 355.
459 Killingbeck KT. 1996. Nutrients in senesced leaves: keys to the search for potential resorption and resorption profi-
460 ciency. Ecology 77: 1716 - 1727.
461 Killingbeck KT, Whitford WG. 1996. High foliar nitrogen in desert shrubs: an important ecosystem trait or defective
462 desert doctrine? Ecology 77: 1728 - 1737.
463 Koerselman W, Meuleman AFM. 1996. The vegetation N: P ratio: a new tool to detect the nature of nutrient limita-
464 tion. J. Appl. Ecol.: 1441-1450.
465 Lal R. 2004. Carbon sequestration in dryland ecosystems. Environ. Manage. 33: 528-544.
466 Lamont BB, Groom PK, Cowling RM. 2002. High leaf mass per area of related species assemblages may reflect low
467 rainfall and carbon isotope discrimination rather than low phosphorus and nitrogen concentrations. Func.
468 Ecol. 16: 403-412.
469 Larcher W. 1995. Physiological Plant Ecology. Ecophysiology and Stress Physiology of Functional Groups. Spring-
470 er, Berlin.
471 Lea PJ, Morot-Gaudry J-F Eds. 2001. Plant Nitrogen. Springer, Berlin.
472 Leegood RC, Lea PJ, Adcock MD, Hausler RE. 1995. The Regulation and Control of Photorespiration. J. Exp. Bot.
473 46: 1397-1414.
474 Ma J, Liu R, Tang L-S, Lan Z-D, Yi L. 2014. A downward CO_2 flux seems to have nowhere to go. Biogeosciences
475 11: 6251 - 6262.
476 McCulley RL, Jobbágy EG, Pockman WT, Jackson RB. 2004. Nutrient uptake as a contributing explanation for
477 deep rooting in arid and semi-arid ecosystems. Oecologia 141: 620-628.
478 McDowell SCL. 2002. Photosynthetic characteristics of invasive and noninvasive species of *Rubus* (Rosaceae. Am.
479 J. Bot. 89: 1431-1438.
480 McKey D. 1994. Legumes and nitrogen: the evolutionary ecology of a nitrogen-demanding lifestyle. Advances in
481 Legume Systematics 5: 211-228.
482 McLachlan, G. J. 2004. Discriminant Analysis and Statistical Pattern Recognition. Willey Series in Probability and
483 Statistics. Wiley-Interscience. A John Wiley & Sons, INC., Publication. New York.
484 Menge DNL, Levin SA, Hedin LO. 2008. Evolutionary tradeoffs can select against nitrogen fixation and thereby
485 maintain nitrogen limitation. Proceedings of the National Academy of Sciences 105: 1573-1578.
486 Mueller-Dumbois D, Ellenberg H. 1974. Aims and Methods of Vegetation Ecology. Wiley, New York.
487 Nieder R, Benbi DK. 2008. Carbon and nitrogen in the terrestrial environment. Springer Science & Business Media.
488 Niklas KJ, Cobb ED. 2005. N, P, and C stoichiometry of Eranthis hyemalis (Ranunculaceae) and the allometry of
489 plant growth. Am. J. Bot. 92: 1256-1263.
490 Nobel PS, Bobich EG. 2002. Plant frequency, stem and root characteristics, and CO2 uptake for Opuntia acantho-
491 carpa: elevational correlates in the northwestern Sonoran Desert. Oecologia 130: 165-172.
492 Nobel PS, Loik ME, Meyer RW. 1991. Microhabitat and diel tissue acidity changes for two sympatric cactus species
493 differing in growth habit. The Journal of Ecology: 167-182.
494 Noy-Meir I. 1973. Desert ecosystems: environment and producers. Ann. Rev. Ecol. Syst. 4: 25-51.
495 Ogle K, Reynolds JF. 2004. Plant responses to precipitation in desert ecosystems: integrating functional types, puls-
496 es, thresholds, and delays. Oecologia 141: 282-294.
497 Osmond CB, Winter K, Ziegler H. 1982. Functional significance of different pathways of CO2 fixation in photosyn-
498 thesis. Physiological plant ecology II. Springer, pp. 479-547.
499 Osnas JLD, Lichstein JW, Reich PB, Pacala SW. 2013. Global leaf trait relationships: mass, area, and the leaf eco-
500 nomics spectrum. Science 340: 741-744.

501 Patten DT, Dinger BE. 1969. Carbon dioxide exchange patterns of cacti from different environments. Ecology 50:
502 686-688.
503 Peñuelas J, Sardans J, Llusia J, Owen SM, Carnicer J, Giambelluca TW, Rezende EL, Waite M, Niinemets U. 2010.
504 Faster returns on 'leaf economics' and different biogeochemical niche in invasive compared with native
505 plant species. Global Change Biology 16: 2171-2185.
506 Phillips DA. 1980. Efficiency of symbiotic nitrogen fixation in legumes. Annual Review of Plant Physiology 31: 29-
507 49.
508 Png GK, Turner BL, Albornoz FE, Hayes PE, Lambers H, Laliberté E. 2017. Greater root phosphatase activity in
509 nitrogen−fixing rhizobial but not actinorhizal plants with declining phosphorus availability. J. Ecol. 105:
510 1246-1255
511 Poulter B, Frank D, Ciais P, Myneni RB, Andela N, Bi J, Broquet G, Canadell JG, Chevallier F, Liu YY. 2014. Con-
512 tribution of semi-arid ecosystems to interannual variability of the global carbon cycle. Nature 509: 600-
513 603.
514 Prăvălie R. 2016. Drylands extent and enviromental issues. A global approach. Earth-Science Reviews 161: 259-
515 278.
516 Raamsdonk LM, Teusink B, Broadhurst D, Zhang N, Hayes A, Walsh MC, Berden JA, Brindle KM, Kell DB,
517 Rowland JJ, Westerhoff HV, van Dam K, Oliver SG. 2001. A functional genomics strategy that uses
518 metabolome data to reveal the phenotype of silent mutations. Nature Biotechnology 19: 45-50.
519 Reich PB, Oleksyn J. 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. Proceedings
520 of the National Academy of Sciences of the United States of America 101: 11001-11006.
521 Reich PB, Oleksyn J, Wright IJ, Niklas KJ, Hedin L, Elser JJ. 2010. Evidence of a general 2/3-power law of scaling
522 leaf nitrogen to phosphorus among major plant groups and biomes. Proceedings of the Royal Society of
523 London B: Biological Sciences 277: 877-883.
524 Reyes-Reyes BG, Zamora-Villafranco E, Reyes-Reyes ML, Frías-Hernandez JT, Olalde-Portugal V, Dendooven L.
525 2003. Decomposition of leaves of huisache (*Acacia tortuoso*) and mesquite (*Prosopis* spp) in soil of the
526 central highlands of Mexico. Plant and Soil 256: 359 - 370.
527 Rzedowski J. 1993. Diversity and origins of the phanerogamic flora of Mexico. In: Ramamoorthy TP, Bye R, Lot A,
528 Fa J (eds), Biological Diversity of Mexico: Origins and Distribution. Oxford University Press, New York,
529 pp. 129-146.
530 Sage RF, Pearcy RW, Seemann JR. 1987. The nitrogen use efficiency of C_3 and C_4 plants III. Leaf nitrogen effects
531 on the activity of carboxylating enzymes in *Chenopodium album* (L.) and *Amaranthus retroflexus* (L.. Plant
532 Physiology 85: 355-359.
533 Sardans J, Peñuelas J. 2014. Climate and taxonomy underlie different elemental concentrations and stoichiometries
534 of forest species: the optimum "biogeochemical niche". Plant Ecology 215: 441-455.
535 Sardans J, Peñuelas J, Ogaya R. 2008. Drought-induced changes in C and N stoichiometry in a Quercus ilex Medi-
536 terranean forest. For. Sci. 54: 513-522.
537 Sardans J, Rivas-Ubach A, Peñuelas J. 2012. The C: N: P stoichiometry of organisms and ecosystems in a changing
538 world: a review and perspectives. Perspectives in Plant Ecology, Evolution and Systematics 14: 33-47.
539 Schlesinger WH. 1997. Biogeochemistry: An Analysis of Global Change. Academic Press, San Diego, CA.
540 Schlesinger WH, Pilmanis AM. 1998. Plant-soil interactions in deserts. Biogeochemistry 42: 169-187.
541 Schlesinger WH, Ward TJ, Anderson J. 2000. Nutrient losses in runoff from grassland and shrubland habitats in
542 southern New Mexico: II. Field plots. Biogeochemistry 49: 69 - 86.
543 Schneider CA, Rasband WS, Eliceiri KW. 2012. NIH Image to ImageJ: 25 years of image analysis. Nat Meth 9:
544 671-675.
545 Shreve F, Wiggins IL. 1964. Vegetation and Flora of the Sonoran Desert. Stanford University Press, Stanford.
546 Sistla SA, Schimel JP. 2012. Stoichiometric flexibility as a regulator of carbon and nutrient cycling in terrestrial
547 ecosystems under change. New Phytol. 196: 68-78.
548 Skujins JJ. 1981. Nitrogen cycling in arid ecosystems. In: Clark FE, Rosswall T (eds), Terrestrial nitrogen cycles.
549 Processes, ecosystem strategies and management impacts. Ecological Bulletin, Stockholm, pp. 477 - 491.
550 Sterner RW, Elser J. 2002. Ecological Stoichiometry. The Biology of Elements from Molecules to the Biosphere.
551 Princeton University Press, Princeton, N. J.
552 Sterner RW, Elser JJ, Fee EJ, Guildford SJ, Chrzanowski TH. 1997. The light: nutrient ratio in lakes: the balance of
553 energy and materials affects ecosystem structure and process. Am. Nat. 150: 663-684.
554 Tao Y, Wu G, Zhang Y, Zhou X. 2016. Leaf N and P stoichiometry of 57 plant species in the Karamori Mountain
555 Ungulate Nature Reserve, Xinjiang, China. Journal of Arid Land 8: 935-947.

Tapia-Torres Y, Elser JJ, Souza V, García-Oliva F. 2015. Ecoenzymatic stoichiometry at the extremes: How microbes cope in an ultra-oligotrophic desert soil. Soil Biol. Biochem. 87: 34-42.
Tschirley FH, Wagle RF, Wagle FF. 1964. Growth rate and population dynamics of jumping cholla (*Opuntia fulgida* Engelm.. Journal of the Arizona Academy of Science 3: 67-71.
Valentine AJ, Kleinert A, Benedito VA. 2017. Adaptive strategies for nitrogen metabolism in phosphate deficient legume nodules. Plant Science 256: 46-52.
Van Devender TR, Felger RS, Fishbein M, Molina-Freaner FE, Sánchez-Escalante J, Reina-Guerrero AL. 2010. Biodiversidad de plantas vasculares. In: Molina-Freaner F, Van Devender TR (eds), Diversidad Biologica del Estado de Sonora. CONABIO - UNAM., México, D. F., pp. 229 - 262.
Vance CP, Heichel GH. 1991. Carbon in N2 fixation: limitation or exquisite adaptation. Annual Review of Plant Biology 42: 373-390.
Vergutz L, Manzoni S, Porporato A, Novais RF, Jackson RB. 2012. Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. Ecol. Monogr. 82: 205-220.
Virginia RA, Jarrell WM. 1983. Soil properties in a mesquite-dominated Sonoran Desert ecosystem. Soil Sci. Soc. Am. J. 47: 138-144.
Virginia RA, Jarrell WM, Whitford WG, Freckman DW. 1992. Soil biota and soil properties in the surface rooting zone of mesquite (Prosopis glandulosa) in historical and recently desertified Chihuahuan desert habitats. Biol. Fert. Soils 14: 90 - 98.
West NE. 1981. Nutrient cycling in desert ecosystems. In: Goodall DW, Perry RA, Howes KMW (eds), Arid-land ecosystems: Structure, functioning and management. V.2. Cambridge University Press, Cambridge, pp. 301 - 324.
West NE, Klemmedson JO. 1978. Structural distribution of nitrogen in desert ecosystems. In: West NEaJS (ed), Nitrogen in desert ecosystems. US/IBP Synthesis series.9. Dowden, Hutchinson and Ross, Inc, Stroudsburg.
West NE, Skujins J. 1978. Nitrogen in desert ecosystems. US/IBP Synthesis series. 9. Dowden, Hutchinson and Ross, Inc., Stroudsburg.
Westoby M, Wright IJ. 2006. Land-plant ecology on the basis of functional traits. Trends Ecol. Evol. 21: 261-268.
Wolf AA, Funk JL, Menge DNL. 2017. The symbionts made me do it: legumes are not hardwired for high nitrogen concentrations but incorporate more nitrogen when inoculated. New Phytol. 213: 690-699.
Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets U, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R. 2004. The worldwide leaf economics spectrum. Nature 428: 821-827.
Wu T-G, Yu M-K, Wang GG, Dong Y, Cheng X-R. 2012. Leaf nitrogen and phosphorus stoichiometry across forty-two woody species in Southeast China. Biochemical Systematics and Ecology 44: 255-263.
Yang X, Chi X, Ji C, Liu H, Ma W, Mohhammat A, Shi Z, Wang X, Yu S, Yue M, Tang Z. 2016. Variations of leaf N and P concentrations in shrubland biomes across northern China: phylogeny, climate, and soil. Biogeosciences 13: 4429-4438.
Yuan ZY, Chen HY. 2015. Decoupling of nitrogen ahd phosporus in terrestrial plants associated with global changes. Nature Climate Change 5: 465-469.

598 TABLES.

599

600 Table 1. Species percentages in the group categories and their mean percent cover. Percent cover was averaged
601 separately for the herb, shrub and tree strata. Herbs and vines were rarely sampled.

602

Group	Cover %	Species %
Functional group		
Vines	1.33	5
Cacti	5.00	16
Forbs	19.45	10
Herbs	12.63	19
Shrubs, non-fixing	10.38	22
Shrubs, BNF	18.61	4
Trees, non-fixing	7.80	14
Trees, BNF	15.35	10

603

604

605

606 Table 2. Means and standard errors of foliar mass concentrations (mg g^{-1}) and stoichiometric ratios of Sonoran
607 Desert species assembled by functional group. Different letters indicate significant differences at $p<0.001$.

608

Functional group	C		N		P		C:N		C:P		N:P	
Trees	445.16 ± 1.97	a	25.74 ± 0.51	a	1.42 ± 0.07	b	18.26 ± 0.37	b	355.01 ± 19.05	a	19.25 ± 1.19	a
Shrubs	442.12 ± 2.94	ab	25.89 ± 0.78	a	1.50 ± 0.06	b	18.68 ± 0.62	b	332.85 ± 17.35	ac	17.72 ± 0.77	ab
Subshrubs	433.16 ± 2.69	b	25.63 ± 1.10	a	2.11 ± 0.17	a	18.71 ± 0.84	b	287.53 ± 34.85	b	15.74 ± 1.74	bc
Grasses and herbs	413.24 ± 2.16	c	15.01 ± 1.07	b	2.13 ± 0.16	a	34.72 ± 2.86	a	224.71 ± 20.66	bc	8.05 ± 1.31	d
Cacti	375.70 ± 3.36	d	11.01 ± 0.87	c	1.33 ± 0.21	b	37.8 ± 2.62	a	365.33 ± 72.04	abc	10.04 ± 1.57	cd
BNFixer	447.45 ± 2.52	a	25.63 ± 0.45	a	1.45 ± 0.08	a	18.16 ± 0.38	b	353.71 ± 17.94	a	19.36 ± -0.88	a
Non fixer	428.87 ± 1.94	b	22.74 ± 0.66	b	1.69 ± 0.07	a	23.06 ± 0.88	a	312.71 ± 16.29	b	15.71 ± 0.85	b
Evergreen leaves	447.07 ± 3.69	a	25.10 ± 0.54	a	1.35 ± 0.09	b	18.54 ± 0.47	b	380.74 ± 30.19	a	19.34 ± 1.12	a
Deciduous leaves	435.63 ± 1.52	b	24.20 ± 0.58	a	1.71 ± 0.06	a	21.11 ± 0.68	b	309.29 ± 13.21	b	16.62 ± 0.76	a
Succulent leaves	375.70 ± 3.36	c	11.01 ± 0.87	b	1.33 ± 0.21	ab	37.8 ± 2.62	a	365.33 ± 72.04	ab	10.04 ± 1.57	b
Non Invasives	441.60 ± 1.47	a	25.80 ± 0.43	a	1.56 ± 0.05	b	18.38 ± 0.33	c	333.84 ± 14.25	a	17.93 ± 0.75	a
Pioneers	424.77 ± 5.47	b	21.44 ± 1.24	b	1.70 ± 0.14	ab	23.86 ± 1.41	b	320.89 ± 28.84	a	15.12 ± 1.17	a
Invasives	409.89 ± 2.78	c	14.58 ± 1.03	c	2.05 ± 0.17	a	35.38 ± 2.74	a	224.71 ± 25.31	a	8.05 ± 1.61	b
All species	434.80 ± 1.83		23.66 ± 0.52		1.62 ± 0.06		21.43 ± 0.66		324.66 ± 13.87		16.78 ± 0.73	

609

610

611

612 Table 3. Mean differences in leaf attributes and stoichiometry ratios between legumes (N_2-fixing and non-fixing)
613 with BNF and non-fixing plant species. Significant differences at $p<0.001$ (**) and $p<0.05$ (*).
614

Variable	Δ Legume - N_2 fixer	Δ Legume - Other spp
C	2.13	10.66
N_{mass}	0.21	2.94 *
P	-0.06	-0.52 **
C:N	0.97	-2.84
C:P	19.52	71.25 *
N:P	0.47	4.57 *
N_{area}	0.21	0.92 **

615
616
617
618

FIGURES.

Figure 1. Location of the study area (dark gray) in the Sonoran Desert (grey) (modified from Shreve and Wiggins 1964).

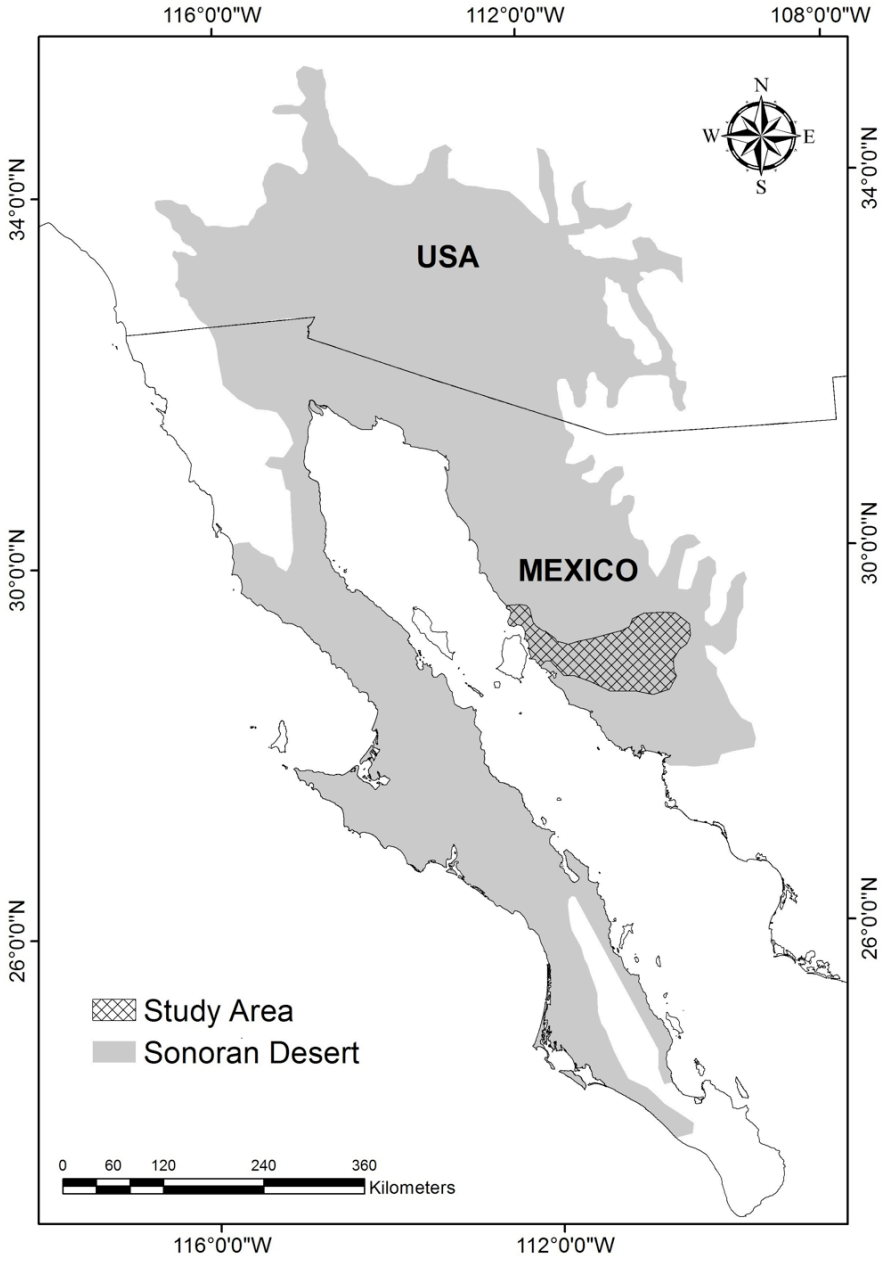
Figure 2. Log transformed correlation of foliar nitrogen (N) with phosphorous (P) mass concentrations of nitrogen fixing (BNF) species and non-fixers. Points are means for each species ($y=0.3792x + 1.2746$; $r^2=0.152$; $p=0.05$).

Figure 3. Log transformed correlation of foliar P mass concentration with C:N stoichiometric ratio of BNF species and non-fixers ($y=-0.3758x + 1.3619$; $r^2=0.164$; $p=0.04$).

Figure 4. Multivariate discriminant analysis for species in the functional groups. Analysis by species colonizing potential (A) and BNF plus colonizing potential (B).

641 Figure 1.

642



643

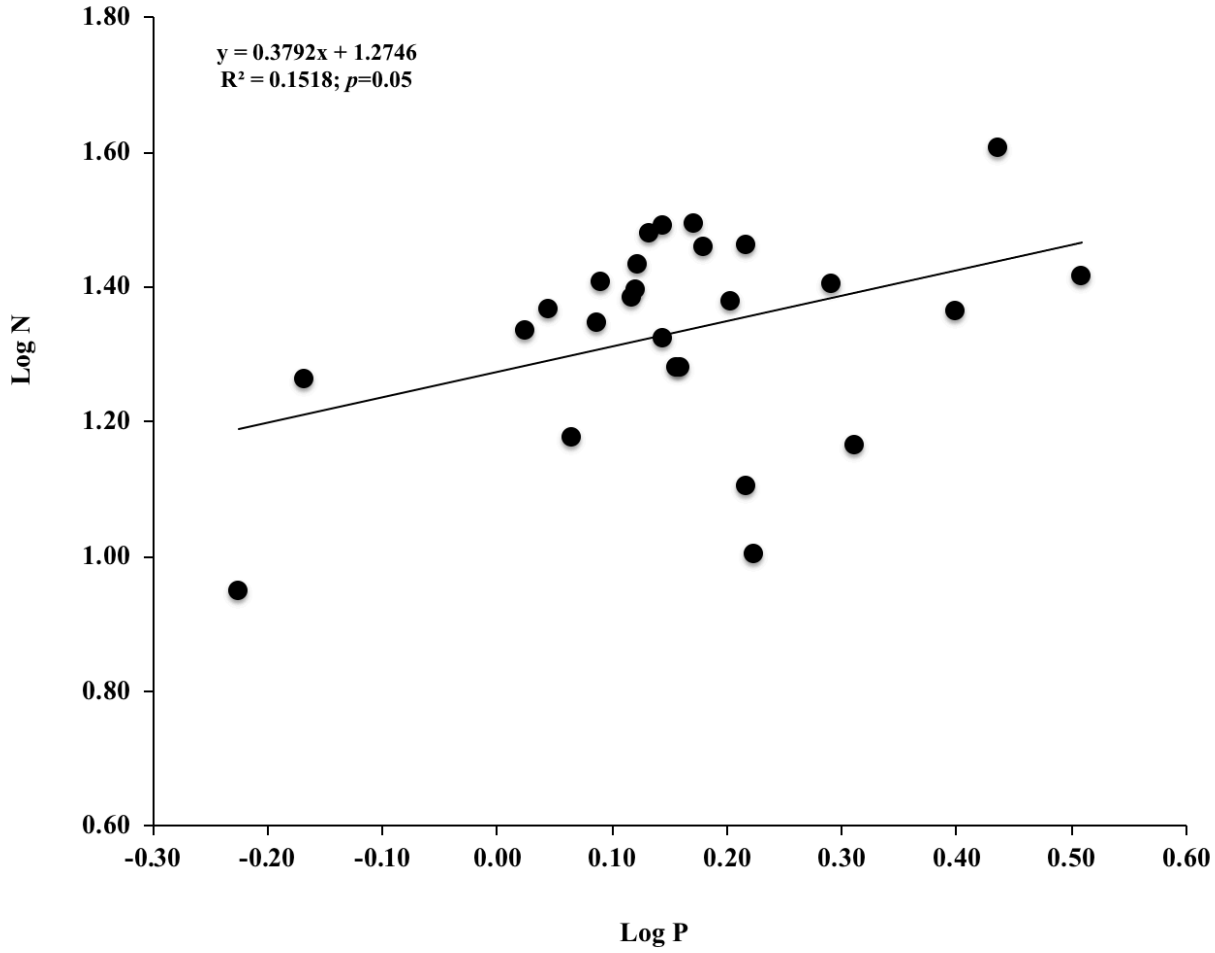
644

645

646

647 Figure 2.

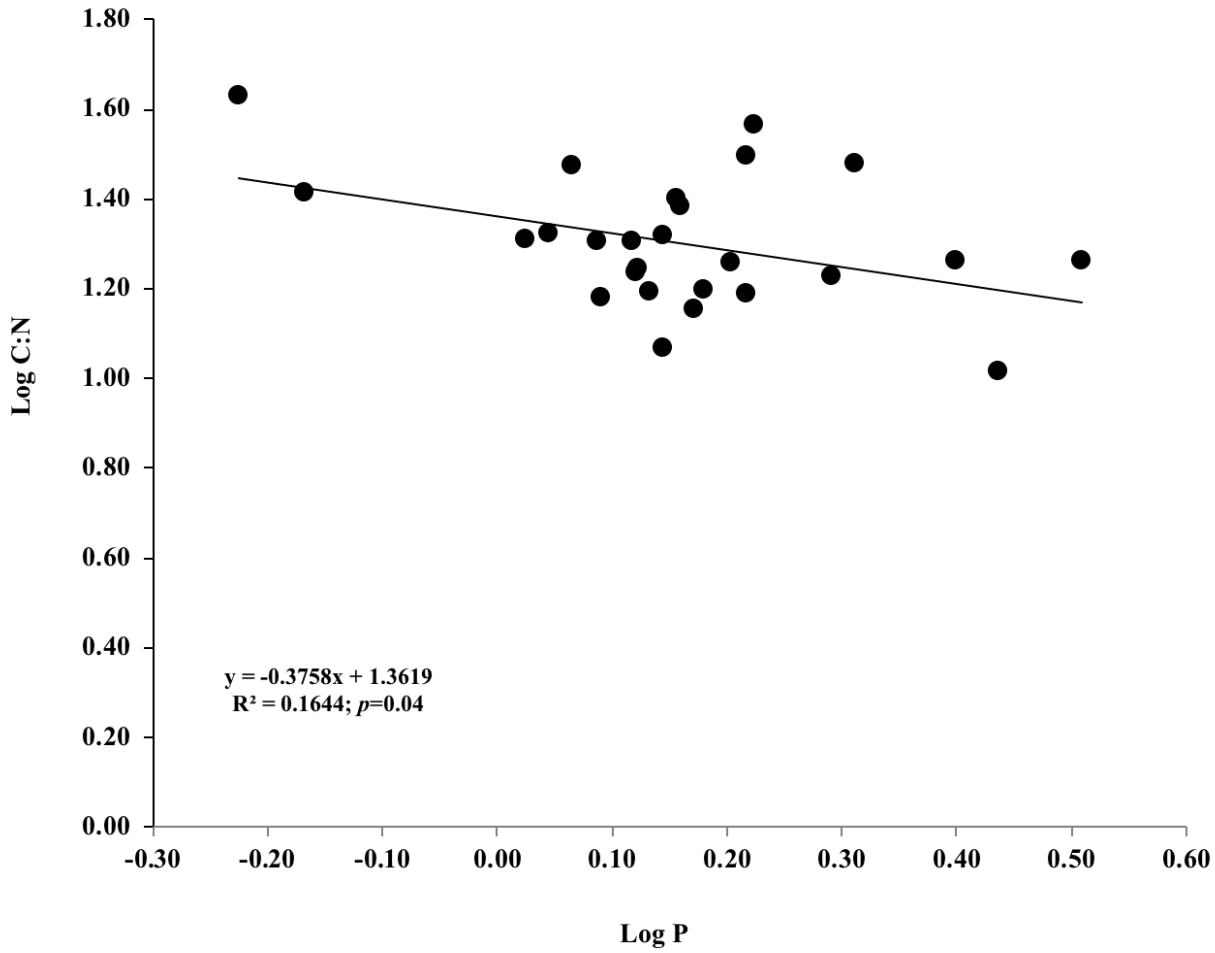
648
649



650
651
652

653 Figure 3.

654

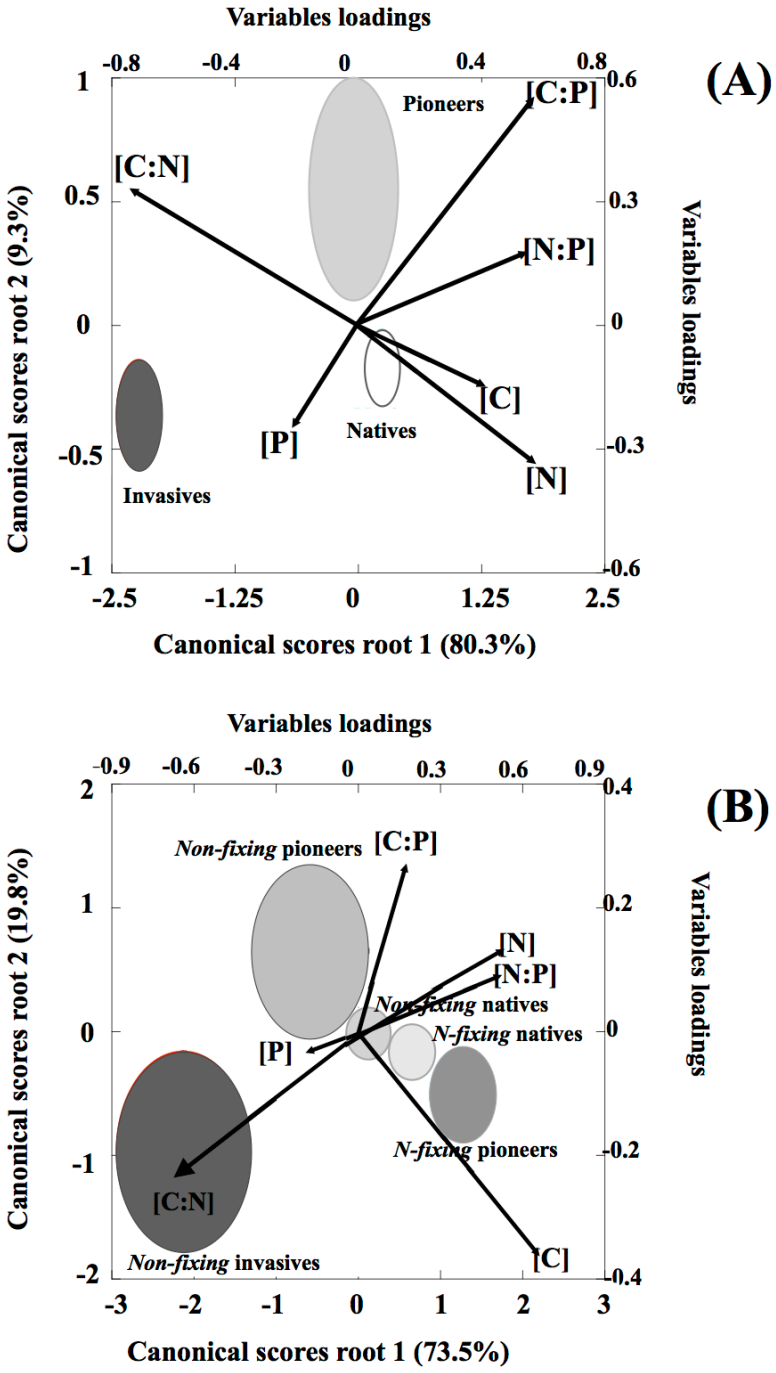


655

656

657

658 Figure 4.



659
660
661
662

663 Supplementary data Table 1. Elemental and stoichiometric ratios of the dominant species in the Sonoran Desert.

664

SPECIES	N-*fixing*	Invasiveness	LMA	C	N	P	C:N	C:P	N:P
			g m^{-2} ± s.d.	mg g^{-1} ± s.d.	mg g^{-1} ± s.d.	mg g^{-1} ± s.d.	± s.d.	± s.d.	± s.d.
Abutilon abutiloides	**N**	**NI**	71.4 ± 6.9	437.6 ± 4.67	14.6 ± 0.71		30.1 ± 1.70		
Acacia cochliacantha	**Y**	**PI**	62.7 ± 6.5	466.5 ± 3.64	30.2 ± 1.83	1.4 ± 0.15	15.5 ± 0.94	344.9 ± 37.29	22.3 ± 3.15
Acacia constricta	**Y**	**NI**	99.5 ± 5.8	454.0 ± 6.05	26.8 ± 1.36				
Acacia cymbispina	**Y**	**PI**	73.5 ± 13.5	486.8 ± 11.55	23.4 ± 3.08	1.2 ± 0.36	21.0 ± 2.23	459.3 ± 144.92	22.2 ± 7.87
Acacia greggii	**Y**	**NI**	80.3 ± 30.4	465.2 ± 7.72	29.9 ± 6.12				
Ambrosia cordifolia	**N**	**PI**	34.7 ± 10.3	414.6 ± 14.56	40.5 ± 5.60	2.8 ± 0.48	10.4 ± 1.69	155.0 ± 36.68	15.1 ± 4.10
Ambrosia deltoidea	**N**	**NI**	85.1 ± 11.9	470.3 ± 7.95	26.0 ± 2.71	3.3 ± 0.44	18.3 ± 2.11	146.6 ± 17.18	8.1 ± 1.06
Brassica tournefortii	**N**	**I**	50.6 ± 5.2	453.6 ± 9.63	26.7 ± 7.38				
Bursera fagaroides	**N**	**NI**	69.7 ± 6.5	443.7 ± 4.13	18.6 ± 1.39		22.5 ±		
Bursera hindsiana	**N**	**NI**	85.6 ± 5.5			1.4 ± 0.08			
Bursera laxiflora	**N**	**NI**	54.6 ± 13.8	434.7 ± 10.71	21.2 ± 2.15	1.4 ± 0.37	19.5 ± 0.87	318.0 ± 87.11	16.4 ± 5.02
Bursera microphyllum	**N**	**NI**	109.0 ± 6.0			1.2 ± 0.05			
Caesalpinia pumila	**N**	**PI**	79.9 ± 28.0	447.3 ± 12.06	29.3 ± 7.42	1.6 ± 0.39	15.9 ± 3.21	302.7 ± 68.88	19.2 ± 2.89
Celtis pallida	**N**	**NI**	89.2 ± 9.2	359.8 ± 17.70	30.9 ± 1.63	1.4 ± 0.26	11.7 ± 1.04	224.0 ± 12.98	19.3 ± 1.16
Cenchrus ciliaris	**N**	**I**	66.8 ± 24.8	390.1 ± 119.62	14.0 ± 8.42	1.9 ± 0.77	33.4 ± 15.60	414.5 ± 633.93	17.6 ± 31.90
Cercidium floridum	**N**	**NI**	78.4 ± 2.9	430.2 ± 13.00	30.9 ± 4.83				
Cercidium microphyllum	**N**	**NI**	118.4 ± 27.7	443.8 ± 9.53	22.7 ± 5.15	1.3 ± 0.26	20.6 ± 5.62	391.0 ± 112.21	20.6 ± 8.84
Cercidium praecox	**N**	**NI**	71.6 ± 6.0	433.6 ± 14.68	36.0 ± 8.86				
Cerdidium floridum	**N**	**NI**	81.0 ± 11.5	408.0 ± 22.06	29.4 ± 3.75				
Croton sonorae	**N**	**NI**	66.8 ± 16.1	441.7 ± 18.36	31.0 ± 1.85	1.5 ± 0.29	14.3 ± 1.15	300.8 ± 62.22	21.0 ± 3.02
Cylindropuntia fulgida	**N**	**PI**		369.0 ± 31.96	11.2 ± 4.82	1.7 ± 0.37	33.3 ± 8.34	225.2 ± 43.49	7.1 ± 2.23
Cylindropuntia versicolor	**N**	**PI**		375.1 ± 7.96	9.0 ± 1.95	0.6 ± 0.06	40.9 ± 6.60	620.9 ± 67.83	15.3 ± 0.82
Encelia farinosa	**N**	**PI**	88.6 ± 17.9	418.2 ± 12.53	23.7 ± 5.46	2.6 ± 0.86	16.6 ± 2.42	176.9 ± 49.17	10.6 ± 2.45
Eysenhardtia orthocarpa	**Y**	**NI**	66.7 ± 15.4	453.4 ± 5.34	29.8 ± 4.16				
Fouquieria diguetii	**N**	**NI**	74.3 ± 3.9	443.7 ± 3.10	15.0 ± 2.11	1.2 ± 0.36	29.9 ± 4.52	396.3 ± 140.62	13.0 ± 2.83
Fouquieria macdougalii	**N**	**NI**	44.5 ± 6.2	456.6 ± 6.09	19.1 ± 2.21	1.5 ± 0.22	24.1 ± 2.84	319.2 ± 54.63	13.3 ± 2.42
Guaiacum coulteri	**N**	**NI**	109.5 ± 6.1	471.1 ± 5.42	18.4 ± 2.65	0.7 ± 0.10	26.0 ± 3.73	699.4 ± 122.06	27.4 ± 6.61
Ipomoea arborescens	**N**	**NI**	36.6 ± 10.6	434.2 ± 18.76	32.2 ± 7.86				
Jatropha cardiophylla	**N**	**NI**	49.6 ± 11.2	443.0 ± 10.03	30.3 ± 9.04	1.8 ± 0.71	17.9 ± 6.32	284.9 ± 99.82	16.5 ± 5.07
Jatropha cinerea	**N**	**NI**	54.1 ± 2.4			1.6 ± 0.19			
Jatropha cordata	**N**	**NI**	41.1 ± 3.6	427.4 ± 10.41	26.0 ± 6.48	2.2 ± 0.93	17.3 ± 4.34	262.3 ± 211.01	17.0 ± 16.49
Larrea tridentata	**N**	**PI**	110.6 ± 21.1	477.9 ± 15.87	19.1 ± 2.13	1.5 ± 0.36	26.4 ± 3.26	349.1 ± 89.31	13.5 ± 4.27
Lysiloma divaricata	**Y**	**NI**	67.8 ± 30.4	430.8 ± 162.48	22.1 ± 10.20	1.4 ± 0.47	19.1 ± 5.66	383.8 ± 110.85	20.8 ± 6.74
Mimosa laxiflora	**Y**	**NI**	72.6 ± 16.1	416.2 ± 76.79	23.7 ± 7.30	1.7 ± 0.39	18.3 ± 3.96	287.7 ± 93.83	16.3 ± 5.91
Olneya tesota	**Y**	**NI**	79.9 ± 13.1	405.8 ± 95.26	23.9 ± 6.92	1.4 ± 0.51	17.9 ± 2.98	351.7 ± 161.08	19.1 ± 5.59
Phaulothamnus spinescens	**N**	**NI**	83.6 ± 10.7	383.0 ± 10.80	26.2 ± 7.92	1.3 ± 0.30	15.5 ± 4.40	260.1 ± 15.28	17.8 ± 5.48
Prosopis velutina	**Y**	**NI**	121.0 ± 24.6	472.8 ± 18.61	27.2 ± 4.15	1.4 ± 0.70	17.6 ± 2.39	368.2 ± 126.42	20.4 ± 5.30
Senna pallida	**N**	**NI**	59.3 ± 18.3	436.5 ± 9.54	22.6 ± 7.04	1.2 ± 0.66	23.7 ± 6.76	468.3 ± 254.27	21.3 ± 14.66
Total general			80.2 ± 30.4	427.5 ± 68.54	23.0 ± 8.98	1.6 ± 0.87	21.9 ± 9.59	344.2 ± 224.06	17.1 ± 10.98

665

666